

The Syncarp of *Artocarpus* — a unique biological phenomenon

by

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The unique compound fruit or syncarp of *Artocarpus* is a fascinating object of study, both for its basic morphology and for its structural and functional diversity. The opportunity that was given to me as a student of Professor Corner to continue his studies on *Artocarpus* and carry out a revision of the genus (Jarrett 1959a, 1959b, 1960) is one that I shall always appreciate. In honouring him in this volume it may be of value to provide a general consideration of the syncarp, drawing together facts that became somewhat scattered in my monograph. The insights into both its internal structure and its biological significance originated with Professor Corner. The revisionary work extended knowledge of the syncarp structure to nearly all species of the genus and made it possible to place the variations observed in a more detailed taxonomic framework.

If one turns first to the morphology, it is found that in *Artocarpus* the compound inflorescence of the Moraceae is condensed into capitate, unisexual inflorescences in which each of the numerous perianths contains a single stamen or ovary. In the male inflorescence the perianths remain free (as they do in both sexes in the allied genus *Prainea*) but in the female head the perianths are more or less completely fused. Where the fusion is only partial it occurs in a highly specialized manner, which is not evident until the syncarp is dissected. It can then be seen that each perianth has a proximal free tubular region with a broad lumen enclosing the ovary. Distally, however, the perianths are early adnate to their neighbours, either fusing with them completely or leaving the perianth apex free. They thus form a continuous external wall to the syncarp which has considerable mechanical strength and is pierced only by the narrow lumen in each perianth through which the style is exerted. Passing from the axis to the outer surface, each perianth thus has either two or three zones, free—fused or free—fused—free. The latter condition was illustrated by Corner (1939) for *A. integer* (Thunb.) Merr. and *A. heterophyllus* Lam. The varying internal structure of the syncarp and some aspects of its external appearance are illustrated below.

In other species, however, the fusion between the perianths is complete or, alternatively, it may be said that the ovaries are enclosed in cavities in a receptacle in which axial and floral elements are not clearly distinguishable.

This then is the basic structure of the compound syncarp of *Artocarpus*, but such a highly specialized and apparently restrictive ground plan can, nevertheless, allow considerable morphological and biological diversity, especially in those species in which the perianths remain free proximally. Monographic study of *Artocarpus* showed that these variations could be linked with the taxonomic subdivision of the genus in which other characters, especially details of leaf anatomy, were taken into consideration, although it also became evident that some parallel evolution had occurred in the syncarp.

Thus a primary taxonomic subdivision into two subgenera, *Artocarpus* and *Pseudojaca*, which can readily be made on the basis of spirally arranged *versus* alternate and distichous leaves, and amplexicaul *versus* lateral stipules, can be

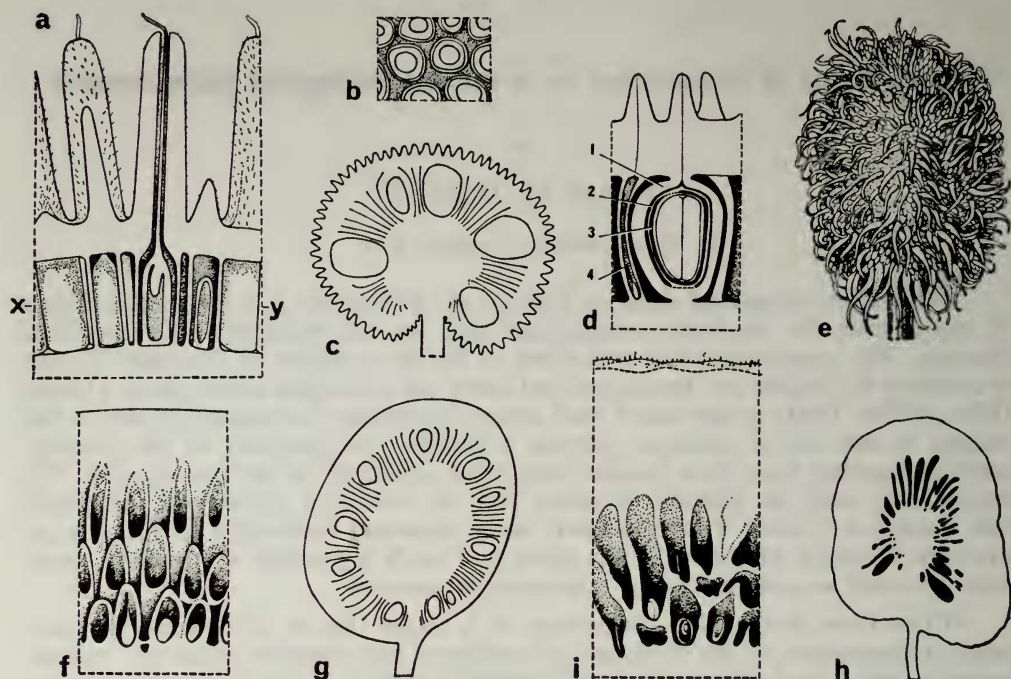


Fig. 1. The syncarp in *Artocarpus*. Subg. *Artocarpus*. *A. hispidus*. a, b, longitudinal section and tangential section in plane x-y at anthesis, $\times 10$; c, longitudinal section at maturity, $\times \frac{1}{2}$; d, part of the same (1, fruiting perianth; 2, ovary; 3, testa; 4, unexpanded perianth), $\times 1$. *A. elasticus*. e, submature head, $\times \frac{1}{2}$. Subg. *Pseudojaca*. *A. peltatus* Merr. f, oblique section at anthesis (perianths free proximally), $\times 2\frac{1}{2}$; g, longitudinal section at maturity, $\times \frac{1}{2}$. *A. fulvicortex* Jarrett. h, oblique section at anthesis (perianths completely fused), $\times 1$; i, part of the same, $\times 3$. a-d redrawn from Jarrett (1959a).

correlated quite closely with syncarp characters. In subg. *Artocarpus* the syncarp is usually ellipsoid or cylindric and the perianths are nearly always free both proximally and at the apex. Most species can in fact be identified by the perianth apices alone (cf. Jarrett, 1959b, f. 16). In subg. *Pseudojaca*, on the other hand, the syncarp is much more uniform in appearance. It is either subglobose or shallowly lobed with a smooth or papillate surface and although in most species the perianths are free proximally, there are several in which they are completely fused.

Artocarpus subg. *Artocarpus* was further subdivided (Jarrett, 1959b) into two sections based mainly on characters of the inflorescence, including those of the embryo, and into several series based primarily, though not solely, on the distinctive, microscopic, capitate hairs on the leaves. Considered biologically and morphologically, three different syncarp types can be recognised in the subgenus corresponding with one or more of these taxonomic subdivisions, while subg. *Pseudojaca* forms a fourth type to which three species from subg. *Artocarpus* (ser. *Rugosi*) should also be referred.

The biological evolution of the syncarp has apparently proceeded in two different directions. It is, of course, indehiscent and is broken down only by the frugiferous mammals and birds that feed upon it or by decay. Nevertheless it can be attractive either as a whole, if the entire syncarp is more or less fleshy, or for the individual fruiting perianths in species where the free proximal region of the perianth is hypertrophied.

The least specialized condition of the syncarp would seem to be found in a number of species in subg. *Artocarpus* sect. *Artocarpus* in which the distal regions of the perianths forming the external wall of the syncarp and the free perianth apices are fleshy but more or less firm while the free proximal regions are thin-walled or only slightly hypertrophied (but sweet and juicy at least in *A. elasticus* Blume and *A. sericicarpus* Jarrett). In contrast with this comparatively undifferentiated internal structure the external appearance of these syncarps is remarkably varied, depending on the shape and indumentum of the perianth apices. They range from scarcely projecting so that the surface appears areolate, each areola representing the tip of a perianth, to long drawn-out and flexuous, giving the figurative appearance of the head of a Medusa. Such elongation of the perianth apices is often associated with dimorphism. There is then usually a marked contrast between the short, perforate apices from which the styles emerge and the intermingled solid processes, which may bear distinctive hairs — long, appressed and silky in *A. sericicarpus* but short and patent in *A. elasticus* (Terap in Malaya) and recurved in *A. tamaran* Becc. and *A. multifidus* Jarrett. In *A. teysmannii* Miq., on the other hand, comparatively few of the perianth apices are elongate and intermediates occur. It is interesting to note that this dimorphism is found in one or more (but not all) of the species in each of the three series in Sect. *Artocarpus* (*Incisfolii*, *Angusticarp* and *Rugosi*) which have this type of syncarp and that it apparently represents parallel evolution.

The fourth series in this section (*Cauliflori*) possesses the most remarkable syncarps in the genus. The enormous fruits of *A. heterophyllus* Lam. (Jack) and *A. integer* (Thunb.) Merr. (Chempedak), which are borne on the trunk and larger branches, may measure as much as one metre in length and half a metre across. The very numerous seeds are enclosed in the strongly hypertrophied proximal free region of the perianths and in the Chempedak (but not the Jack) these separate from the wall and the core at maturity, falling out when the baggy syncarp is cut open. The taste and smell is highly characteristic of each species and was described by Corner (1939) as "sickly sweet" in the Jack and much stronger ("of durian and mango") in the cultivated Chempedak (but lacking in the wild var. *silvestris* Corner). The syncarp surface is covered by firm, but not indurated, conical perianth apices.

The smaller, globose or short-cylindric, armoured fruits of sect. *Duricarpus* representing the third type of syncarp in subg. *Artocarpus*, have seeds that are likewise surrounded by succulent, hypertrophied perianths. The free tips of the perianths are, however, woody and, while in some species such as *A. lanceifolius* Roxb. (Keledang) and the pinnate-leaved *A. anisophyllus* Miq. they are merely cylindric, in others such as *A. rigidus* Bl. (Monkey Jack) and the related *A. hispidus* Jarrett, they form tapering spines.

The smooth or papillate, fleshy syncarps of subg. *Pseudojaca* (Tampang in Malay) present a strong contrast to those just described and, as already stated, there is relatively little variation in appearance and morphology. Only in *A. styracifolius* Pierre from southern China is the surface covered by flexuous processes and these appear to be formed from enlarged interfloral bracts. (Bracts are present among the flowers in most species of *Artocarpus* at least in juvenile inflorescences but their heads are usually minute and discoid or infundibuliform.) As regards internal structure, where the proximal portion of the perianths is free it is thin-walled, but in several species, including *A. fulvicortex* Jarrett among Malayan species (Orange-Barked Tampang in Corner, 1940), the perianths are completely fused. Finally a few species in subg. *Artocarpus* such as *A. kemando* Miq. have small fleshy fruits which should be classified biologically with this group.

The biological significance of the syncarp in *Artocarpus* was taken up by Corner in his discussion of the Durian Theory, in which the genus was frequently mentioned (1949, 1954a, 1954b). Vegetatively it shows both massive pachycaul

and slender leptocaul construction and, in particular, the association of the latter with cauliflory in *A. integer* and *A. heterophyllus*. The compound syncarp, moreover, shows striking parallels in some species with fruits of the Durian type. The surface may be armoured but here this is by perianth apices rather than by simple spines; the fruit may be strong smelling as, for example, in *A. elasticus*, *A. heterophyllus* and *A. integer*; and, finally, fleshy perianths can take on the function of an aril (Corner, 1962). However, other parallels may also be seen in the genus since the fleshy syncarp. of subg. *Pseudojaca* can be compared with a berry, although the flesh is formed from the perianths and axis rather than from the carpel wall. It may be added that in the allied genus *Prainea*, in which the perianths remain free in the female inflorescence, the few that form seeds and project from the surface each resemble a single-seeded berry in which, again, the flesh is formed by the perianth.

It might be assumed that these biological variations in the syncarp would be reflected in marked differences in the animals acting as distributors. However, while differences do exist they are not very clear-cut. Precise information is scanty and mainly derived from cultivated trees, which is not surprising since in the forest *Artocarpus* is usually widely scattered. However, it is clear from observations gathered together by Ridley (1930) and others made by Corner (1939, 1940) that it is the attractive flesh, variously dispersed in the syncarp, that brings about the distribution of the seeds. Arboreal mammals, especially monkeys and civet cats break open the larger fruits, nibbling the juicy perianths and scattering at least some of the seeds. Docters van Leeuwen (1935) also records several species including two of the most important cultivated species, Chempedak & Breadfruit, as being eaten by bats, a fact first mentioned by Rumphius. Ridley suggests that the cauliflorous fruits are eaten by wild pig, cattle and elephants. The smaller fleshy fruits may be eaten by birds or bats and could be carried off whole and thus more widely distributed. However the distribution patterns of the species, which were mapped in my monograph, suggest that water is a strong barrier to dispersal, as might be expected with such large seeds lacking in dormancy.

The uniqueness of the syncarp in *Artocarpus* lies in the partial fusion between tubular perianths which exists in most species. This character has made possible the differentiation for attractive or protective functions of the proximal and distal regions of the perianth and hence the remarkable biological parallels between this compound fruit and syncarps derived from a single flower. It is evident that field observations are still needed to enrich our biological knowledge of this diverse genus.

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